MINOT (C. S.)

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MORPHOLOGY OF THE EAR.

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MORPHOLOGY OF THE EAR.

By CHARLES SEDGWICK MINOT.

The present article is the first of a proposed series, intended to present a comprehensive summary of our knowledge of the structure of the ear. A great amount of work has been devoted to this subject, and many important discoveries have been made; yet there is, I believe, no recent general review of the matter. The articles will be entirely compilations. It is my intention to ultimately revise them to form a chapter in a work on comparative histology.

The articles will all be illustrated, and will take up the different classes of animals in their proper order. The invertebrates will require but a brief treatment.

1. The Medusæ.

The lowest animals known to have auditory organs are the medusoid jelly-fishes (*Discophori*). These animals have the general shape of a concavo-convex disk, and the edge of the disk bears various tentacles, contains a circular tube known as the *ring canal*, and is also prolonged into a thin flap—the *velum*. Besides these structures, this edge bears certain small bodies of two kinds: one,

pigmented spots regarded as ocelli; the other, containing concrements (otoliths), and on that account recognized as auditory organs. In most jelly-fishes the two sensory organs are quite separate, but in the Acraspeda an ocellus and *Hörkörper* are placed together on a common stalk.

The sensory bodies are easily found; thus, in the common *Aurelia* there are sixteen notches in the edge of the disk, in each notch two little lappets, and between the bases of each pair is a projecting sensory body with both pigment and concrement-spot.

The auditory organs of Medusæ have been elaborately investigated by the brothers Hertwig,[1] and the presentation of their results is the first object of the present article. The sense-corpuscles have been long known to naturalists, and several of the earlier writers have described their varying distribution and numbers in several species. There are also fragmentary observations upon their histological structure recorded by certain authors, notably Gegenbaur, Fritz Müller, Kölliker, and Hensen. Haeckel has also published descriptions of them, but unfortunately is grossly in error on important points. The brothers Hertwig have, with rare skill and patience, investigated these organs and determined their principal homologies. They examined both living specimens, microscopic sections, and macerated tissues. To harden the tissues for cutting they were placed in 0.5 per cent. solution of osmic acid for five to fifteen minutes, then colored in diluted Beale's or picrocarmine, and preserved in weak alcohol. For cutting, they were embedded between two pieces of liver, previously hardened in alcohol and cut out to fit around the tissue. Several of their figures have been engraved for a treatise upon "Comparative Histology," and, by a special arrangement due to the liberality of the editor of this journal, are herewith reproduced. The velum, *V*, when represented, is drawn in an unnatural position, that is, turned outward, instead of reflected back under the edge of the disk and the ring canal, *R*.

The auditory organs are of two types: the first type is found in the *Vesiculata*, and is developed from the ectoderm; the second

[1] Oscar and Richard Hertwig: Das Nervensystem und die Sinnesorgane der Medusen. Monographisch dargestellt. Pp. x. and 186, Taf. I—X. Leipzig, 1878.

type is found in the *Trachymedusæ* and *Acraspeda*, and is developed from both ectoderm and entoderm. The latter type offers the only instances known of the inner germ-layer directly participating in the formation of an auditory organ. It is possible for it to form accessory parts, because it comes into immediate proximity with the ectoderm in several places where the mesoderm is absent. Thus, in Fig. 1, the ring-canal, *R*, as seen in a radial section through the edge of the disk, is formed by an epithelium (entoderm) which runs close up to the ectoderm at the base of the velum, *V*.

The otocysts of the first type present a series of modifications, the simplest form being an open cup on the under side of the velum (Fig. 1, *V*) (the velum being everted). In the higher form the cup is not only deepened, but its opening is contracted until it becomes entirely closed over. We begin our review with the first form as found in *Mitrocoma*, and probably in the American *Tiaropsis*, the auditory organ of which has been described as an eye by Louis Agassiz; and also in *Halopsis*. The two latter genera occur on our coast, and it is to be hoped that some investigator will study them. About eighty auditory cups are found in *Mitrocoma*, in the base of the velum around the edge of the disk or umbrella, there being one between every two main tentacles. A radial section through a cup (Fig. 1) shows its simple structure. The ring-canal, *R*, is cut transversely, and is lined upon its lower surface by large, ciliated, epithelial cells. The ectoderm, *Ec*, comes down from the gelatinous disk above, and consists of very much flattened epithelial cells. When it reaches the level of the ring canal it suddenly becomes a thickened neuro-epithelium, which has upon its free surface (sensory?) hairs, and at its base nerve-fibres and ganglion-cells, as indicated by the dotting in the figure. The ectoderm on the under surface consists of cubical cells. Both parts of the

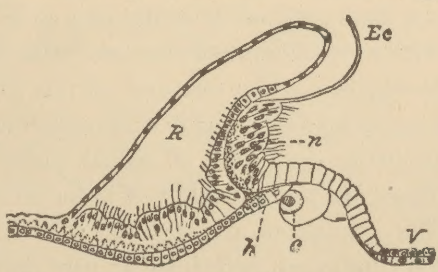

FIG. 1.—*Mitrocoma annæ*.—Radial section through edge of disk and an auditory cup: *R*, ring canal; *Ec*, ectoderm; *n*, neuro-epithelium; *V*, velum; *c*, concrement-cells; *h*, hearing-cells.

outer cell layer extend beyond the lower external angle of the ring canal, forming conjointly a circular flap or velum, *V*, around the edge of the disk. These relations are perhaps more clearly shown in Fig. 4, but can also be followed out in Fig. 3. In most radial sections the velum presents no especial peculiarities; but such a section through an auditory cup shows that the cup is formed by an upward arching of the velum to form a little dome, characterized not only by its shape, but also by striking differentiations of the epitheliums of the velum. The cells of the upper layer are much enlarged (see also Fig. 2, *ec*), their walls very much thickened, so that when the epithelium is viewed from the surface its appearance reminds one of a honey-comb. The contents of the cells are chiefly fluid, with a small nucleus generally in the base of the cell. These cells cease abruptly both toward the neuro-epithelium and the velum. The epithelium of the under side, which makes the lining of the cup, consists of three kinds of cells, running in bands parallel with the ring canal, and therefore cut across in Fig. 1. The outer band is unmodified epithelium, the middle band a variable number of large *concrement-cells*, *c*, the innermost auditory cells (*Hörzellen*), *h*. The concrement-cells are large, projecting above the level of the rest of the epithelium, and are distinguished by containing an irregularly spherical concretion, with a small depression at one point of its surface. The concretion is attached to the free end of the cell, where the cell-nucleus also lies; is soluble in acids without formation of bubbles, and therefore probably composed of calcic phosphate with an organic basis. There are ten to twenty of these cells of various sizes in each cup. The concretions are regarded as otoliths. The third band, nearest the ring canal, is formed by very delicate *Hörzellen*, three to five to each concrement-cell. They have each an auditory hair, while their bases taper down to fine threads.

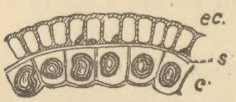

FIG. 2.—*Mitrocoma annæ*—Section through concrement-cells of auditory cup, taken at right angles to radius of disk: *ec*, upper epithelium; *s*, supporting membrane; *c*, concrement-cells.

The essential features, then, of the organ under consideration are: a cluster of *Hörzellen* of typical form, outside of which is a smaller number of concrement-cells, both kinds being developed from the ectoderm of the under side of the velum. The modifi-

cations of the organ are produced by variations in the size and shape of the whole, and in the size, shape, and number of the auditory and concrement-cells.

As before mentioned in the majority of the *Vesiculata*, the cup grows deeper and becomes a closed sack. As this otocyst is essentially the same in all the remaining species of this group studied by the brothers Hertwig, it will suffice to give the results obtained from *Aequorea forskalea*, a species estimated to have the astonishing number of six hundred otocysts. The most important points are illustrated in a radial section (Fig. 3). The ring-canal, *R*, and velum, *V*, occupy the same relative positions as before. The thickened ciliated neuro-epithelium lies just outside the ring-canal. Between the neural band and the base of the velum intervenes the otic vesicle, upon the upper wall of which are the concrement-cells, *c*, usually several irregularly distributed, sometimes only one. On the inner walls are the *Hörzellen*, quite numerous, and larger than in *Mitrocoma*. The lower side is of course not open, but closed by epithelium. The section, however, still plainly indicates how the shutting took place by the gradual approximation of the rim of the cup toward its own centre. This is especially shown by the course of the so-called supporting membrane (Stutzlamella, cf. Fig. 4, *s*), a structureless sheet which lies, on the one hand, between the ectoderm and the ring canal; on the other, between the upper and lower epithelium of the velum. In *Aequorea* the lamella passes over the *Hörzellen* and concrement-cells, and down through the outer wall of the vesicle, but does not pass round below. In other words, the growing together has not extended so far as to include the lamella. The minute structure of the parts requires a short additional description. In the first place, it is to be especially noticed that the outer epithelium of the otocyst is a simple layer, the singular honey-comb-like cells of *Mitrocoma* being

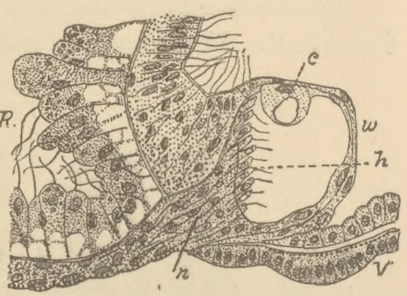

FIG. 3.—*Aequorea forskalea.*—Radial section of an otocyst: *R*, ring canal; *c*, concrement-cells; *w*, wall of the vesicle; *h*, hearing-cells; *V*, velum; *n*, nerve.

absent. The concrement-cells project with rounded ends above the epithelium, contain little protoplasm, and a basally placed nucleus. The concretion is normally pear-shaped (but easily distorted by reagents), the pointed end being attached to the thick membrane over the free end of the cell. The sensory cells, *h*, are small, but may be more easily studied in the allied genera *Obelia* and *Phialidium*. Each cell has one hair, an oval nucleus, a tapering base, and a lamellar projection, running toward the base of the concrement-cell, essentially as in *Mitrocoma*. The hearing-cells have their long axis always oblique, that is, never perpendicular to the surface of the epithelium. The *Hörzellen* sit upon a mass of cells and fibres (Fig. 3, *n*), which also help to close the lower side of the vesicle. The same structure can be detected in the open cup of *Mitrocoma* under the epithelium alongside the auditory cells (Fig. 1, *h*).

We pass now to the second type of auditory apparatus, which is found in the *Trachymedusæ* and *Acraspeda*. The Ocellata have no organ of hearing. In the second type, as in the first, the essential elements are hair-cells and concrement-cells, but the latter are derived, not from the ectoderm, but from the inner germ-layer. The interesting development of the organ was followed by preparations of young *Cunina lativentris*. At a point where the auditory apparatus is to be formed, the lining of the ring canal develops an outgrowth of a few cells, which push the ectoderm out before them. This outgrowth takes place in the midst of the neural epithelium, just above the base of the velum. The cells from the entoderm become constricted off from their connection with the ring canal, and it soon projects like a small tentacle, which ultimately is constricted around its base (Fig. 4, *H*). The ectoderm, covering the

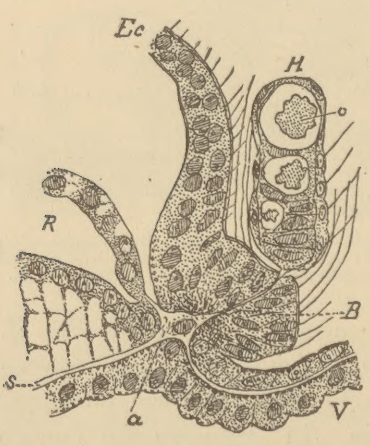

FIG. 4.—*Cunina lativentris*.—Radial section through the auditory knob: *R*, ring canal; *Ec*, ectoderm of the disk; *H*, auditory knob; *c*, concrement; *B*, auditory bolster; *V*, velum; *a*, entodermic cell derived from ring canal; *s*, supporting lamella.

rod or knob, becomes a simple epithelium, as in *Cunina*, etc., or may be developed, in part, into auditory cells, as in the *Geryonidæ* (Fig. 6). The entodermic or axial cells, on the other hand, give rise to the concrements (Fig. 4, *c*).

In the simplest form, found in the Aeginidæ, the neuro-epithelium around the base of the knob, and some of the ectodermal cells upon it, become converted into the sensory cells, bearing long hairs (Fig. 4), which reach up around the sides of the knob. The concretions vary in number; in *Cunina*, there are usually two in the distal ends of the knob. The concrement-cells resemble, in a general way, those of the Vesiculata. The concretion, however, possesses a more crystalline character, which, in some species, is very marked. The axial cells are much flattened and form a single row; the nucleus occupies nearly the whole thickness of the cell. They are separated by a prolongation of the supporting membrane from the ectoderm of the knob, and this membrane extends down through the neuro-epithelium to the cell, *a*, originally a part of the wall of the ring-canal. In this manner a trace of the original connection of the axis, with the entoderm, is permanently preserved. The outer epithelium of the knob bears short hairs, which cross the long, stiff, curving hairs of the auditory bolster (*Gehörpolster*), *B*. From observations on several members of this family, it appears that nerve-fibrillæ enter the knob, and that the hair-bearing cells have tapering bases, which probably become connected with the fibrillæ; hence, it is supposed that the epithelium of the knob has auditory functions.

The essential features of this arrangement then are, that a knob with an entodermic axis grows up at a point in the neuro-epithelium and becomes constricted at its base. The terminal, or the terminal and penultimate cells of the axis, develop concrements of phosphate (?) of chalk with an organic basis. The ectoderm over the knob and around its base is converted into the sensory hair-bearing epithelium. Modifications are produced by variations in shapes and proportions of the part. Thus, in *Aeginopsis mediterranea*, the knob is pear-shaped, with a single large, spherical concrement (cf. Fig. 5); in *Cunina sol maris* the bolster is so prominent that it forms a distinct papilla.

In the family of Trachynemidæ, homologous structures are preserved, with an advance of organization in some forms. The knob is smaller, and there is no distinct bolster, although the epithelium around the base of the knob bears sensory hairs, which, however, are of the same length (in *Aglaura*) as, or shorter (in *Rhopalonema*, Fig. 5) than, the hairs upon the knob. The young of the last-mentioned genus have at first four simple knobs closely similar to those of *Aglaura;* but when older they then acquire eight, which attain a higher differentiation in that a proliferation of the ectoderm takes place, forming a circular wall around the base of the knob. The wall grows upward and gradually closes over the knob, leaving for a long time a small opening (Fig. 5), which, however, ultimately disappears. In this manner a closed otocyst is formed, strikingly similar to that of *Aequorea*, which has a different developmental history. The walls of the otocyst (Fig. 5) are composed of two epithelial layers, and hold a fluid in which the knob is suspended.

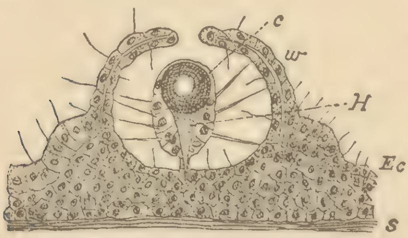

FIG. 5.—*Rhopalonema velatum.*—Horizontal optical section of otocyst, still open: *H*, knobs; *c*, concrement; *w*, wall of vesicle; *Ec*, ectoderm; supporting lamella.

In the Geryonidæ there is a further departure from the primitive form, which causes a very interesting approximation to the otocysts of molluscs and the higher animals. The organs in question are vesicles, which agree in all the essential points of their structure with the otocysts last described (of the Trachynemidæ), but their position is changed from the exposed surface to an inward place, where they are embedded in the gelatinous tissue of the disk. The knob is suspended from the side of the vesicle farthest away from the surface, just as we should expect. The walls of the vessels are lined by a single layer of epithelium, so that we are forced to conclude that the sac was formed by the sinking in of the knob. The axis of the knob consists of two cells, the distal one with a large concrement (Fig. 6, *c*). The ectoderm on one side is simple; on the other side of the knob is differentiated into large hair-cells, *h*, with stout, curving hairs. Owing to the position of

the otocyst the nerve-fibrillæ have to run some distance. They are gathered into two nerves, which pass around the walls of the vessel (Fig. 6, *n* and *n'*), to enter the base of the knob.

The *Acraspeda* have an auditory knob, quite similar to that of the Geryonidæ, but presenting certain important peculiarities, of which only three need be mentioned here: *First*, the otic organ is closely combined with the ocellus, which is placed either directly upon, or in close proximity to, the knob. This relation can be seen in our common *Aurelia*. *Second*, the knob is sunk in a little depression and covered over by two lappets. This disposition is intermediate between the free exposure of the knob and its shutting in in a vesicle entirely closed and embedded in the gelatinous tissue of the disk. *Third*, in some species the otolith is not a compact concretion, but a mass of small, crystal-like deposits (*e. g.*, *Aurelia*), which are deposited in the entodermic axis. Without further details, it is evident these organs belong to the second type we have considered.

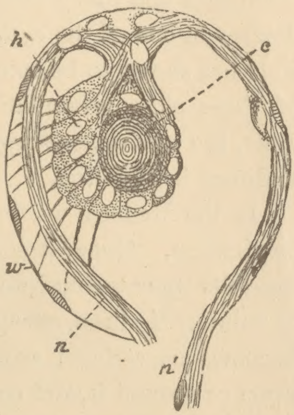

FIG. 6.—*Carmarina hastata*.—Otocyst seen from the surface: *h*, hearing-cells; *c*, concrement; *w*, wall of vesicle; *n* and *n'*, nerves.

The manner in which the knob is developed is essentially the same as for a simple tentacle, which is an ectodermal tube filled with a rod of cells from the ectoderm. We are therefore justified in regarding the auditory knobs as specialized tentacles. They are entirely distinct from the auditory organs of the Vesiculata, which are developed from the velum, as we saw above.

No experiments have yet been made to demonstrate the auditory functions of the organs we have described. Yet their structure leaves little opportunity for questioning the physiological value assigned to them. It is evident that the exposed external position offers no valid objection to the view advanced, for not only does embryology teach us that the auditory organs are developed from the exposed ectoderm, but in some animals, such as the common cray-fish, the ear is an open pit. Positive evidence is offered

by the sensory cells with their long, stiff hairs, and by the concrement-cells, with their mineral deposits, otoliths. It is true that the otoliths of most animals are free bodies in the interior of the otocyst, although they are attached to the walls of the vesicle in the Tunicates and many worms. Yet they probably always arise as a deposit in one of the cells of the epithelial lining of the otocyst, as Fol[1] has shown to be actually the case in certain molluscs. In view of these close resemblances of organization with undoubted otocysts, the concrement-organs must be regarded as unquestionably auditory in function.

In the Medusæ we find, as it were, the auditory organs in their origination. General sensory cells become in the Vesiculata hearing-cells by entering into relation with a concrement-cell. In the remaining Medusæ, excepting the Ocellata, a rudimentary tentacle becomes constricted around its base, sensory cells are developed upon or around it, and concretions (otoliths) are formed in its entodermic axis. Both types acquire a higher development by coming to lie in pits, which may afterward close over, forming shut vesicles filled with fluid.

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[1] **Hermann Fol: Études sur le Développement des Mollusques. Paris, 1875.**